Taste perception and feeding behavior in non-human primates and human populations

Claude Marcel Hladik, Bruno Simmen

Paper published as a review
in : Evolutionary Anthropology, 1996, vol 5 : 58-71
by : C.M. Hladik & B. Simmen

Taste Perception and Feeding Behavior in Nonhuman Primates and Human Populations

CLAUDE MARCEL HLADIK AND BRUNO SIMMEN

Recent advances in taste physiology provide evidence against the traditional "western" notion that there are only four basic tastes. Each substance elicits a singular "signature" on the peripheral taste nerve, but in some cases the signals form separate clusters within the continuum of taste perceptions. We will discuss the taste abilities of nonhuman primates in terms of threshold and above-threshold responses to potential foods. As diets have evolved in species' environments, tastes have responded adaptively in order to maximize energy intake. In turn, food plants have evolved nutrients and toxins in relation to the tasting abilities of consumers. These compounds can be beneficial or harmful in various environments and at different concentrations. This cost-benefit ratio concerns all primates, including *Homo sapiens* populations living at subsistence level, and must be taken into account, together with psychosensory and sociocultural factors, to understand food choices.

Food choices vary drastically across human populations in relation to both environmental and cultural factors. For example, the extreme high-protein and high-fat diet of the Inuit is an obvious response to the foods that, despite recent socioeconomic changes, are available in the arctic environment.[1] In contrast, the high-protein diet of Aka and Baka Pygmies results from a subsistence strategy that does not simply reflect the abundance of game in the African rain forest, since other populations living in the same habitat use different strategies resulting in distinct diets.[2]

One may question the extent to which specific food preferences, built on a common repertoire of available foodstuffs, result from adaptive trends or depend on sociocultural preferences. This issue can be clarified by exploring the perception system from its initial biological foundations, including nonhuman primate evolutionary trends, to its cognitive dimensions, including the symbolic values placed on foods and feeding practices. Observations of the feeding behavior of nonhuman primates conducted during recent decades provide an extensive background against which responses by *Homo sapiens* can be reexamined.[3-5] Because the study of taste physiology has been marked by important recent advances, a brief survey of chemoreception mechanisms and psychosensory responses will be necessary to clarify our subsequent discussion of taste perception in relation to nutrients and toxins in foods.

Claude Marcel Hladik and Bruno Simmen work on feeding behavior as members of an interdisciplinary research team, Anthropologie et Écologie de l'Alimentation, at the Muséum National d'Histoire Naturelle (Brunoy, France). Before creating this CNRS research unit in cooperation with anthropologists, C.M. Hladik carried out field work for more than 20 years, characterizing the dietary adaptations and feeding behavior of wild primates in Africa, America and Asia. Bruno Simmen's research, which is focused on primate taste perception, has combined observation of wild primates, mostly in French Guiana, with behavioral experiments at the Brunoy laboratory.

Key words: sugar perception, taste aversion, salt perception, forest populations, taste acuity

CHEMORECEPTION MECHANISMS

Most foods activate chemoreceptors in both the taste and olfactory systems. The resulting perceptions are simultaneous and cannot easily be separated. For example, the volatile compounds of an orange stimulate the nasal mucosa (especially through the pharynx), whereas the soluble substances of the juice, in contact with the lingual mucosa, elicit a sweet-sour taste response. In common usage, "taste" designates the global taste and odor feeling, even including tactile, trigeminal (irritation from strong acid or chili), and thermal perceptions. There is evidence that such merged stimulations are not restricted to *Homo sapiens*. Indeed, single neurons within the mammalian brainstem (nucleus of the solitary tract) are activated by odor as well as by taste stimuli.[6] Even color can change the quality of flavor. For example, uncolored orange juice is perceived as being less tasty.[7] The convergence of visual, olfactory, and gustatory neural pathways channeled toward the integrative cortical structures[8] obviously contributes to a global perception of food.

However, when considering the taste signal alone, it is necessary to avoid misconceptions. The concept of four basic taste qualities has been laid to rest by many scientists, beginning with Schiffman and Erickson[9] and Faurion.[10,11] Bitterness, sweetness, sourness, and saltiness are semantic descriptors that are common to several societies but they do not have a clear-cut physiological basis. Several substances, such as liquorice, cannot be associated with any of these simple descriptors.[12] However, the theory that there are only four basic taste qualities—an idea that was prevalent for half a century and still is advocated[13]—led to the design of experiments to show, for example, that some fibers of the mammalian taste nerve respond more strongly to sugars and

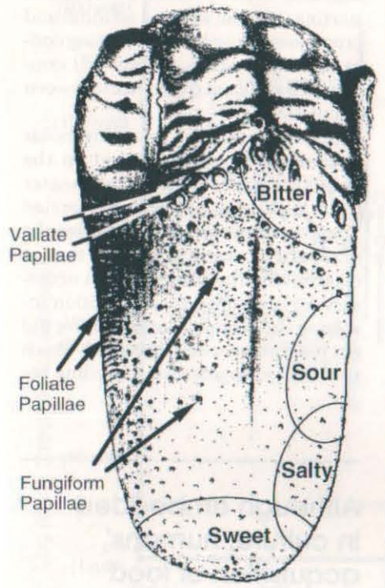


Figure 1. Describing taste stimulation as four separate basic tastes is an oversimplification, although different areas of the human tongue are known to respond best to sugar or other sweeteners, quinine or other bitter substances, sodium chloride, or acids. Most taste cells respond to several substances, sometimes showing a higher affinity for one of them. The topographical responses of the tongue could be related to concentrations of best-responding cells in the taste buds of some papillae.

artificial sweeteners than to other substances.[14] Such partly specialized fibers may start from different areas of the human tongue (Fig. 1) that present higher sensitivity to sugars (or to acid, salt, or bitter substances). The tongue of the chimpanzee exhibits a different morphology[15] from that of the human tongue (Fig. 2), but it may also have areas with partial taste specialization corresponding to the taste nerve fibers that respond mainly to bitter substances, sugars, or salts. This is suggested by the recent work of Hellekant and Ninomiya.[16] However, most sensory cells of the mammalian taste buds show little specificity. They generally respond to several substances, having higher affinities for some of them.[10,17]

The shape of the signal elicited on gustatory nerves is the result of the combined firing of all these cells. It is a kind of signature that differs more or less according to the stereochemical structure of the substance being tasted. This complex initial taste signal can provide a clear-cut psychosensory image in humans,[18] especially when the stimulation is strong. But in many cases, and particularly at low concentrations (when the shape of the signal is incomplete), it is difficult to discriminate among substances eliciting globally similar signals. For instance salt, at low concentration, evokes a taste close to that of sugar.[10] When measuring thresholds, it is crucial not to ignore this complex build-up of the gustatory signal.

There are, nevertheless, categories of substances (e.g. sugars and acids) that elicit taste signals with such similar shapes that it is not easy to discriminate among different products within each category, even at high concentration. The occurrence of such classes of tasty substances among natural products is related to evolutionary trends in food nutrient content and toxicity. The limited number of semantic descriptors in most languages also reflects these taste spaces with blurred contours. Accordingly, we use the familiar terms of sweet, sour, bitter, and salty, bearing in mind that these taste qualities are not discrete entities.

Figure 2. The tongue of a chimpanzee shows a distribution of papillae differing from that on the human tongue. The recent finding in the chimpanzee of nerve taste fibers that respond best to sweet or bitter substances (as perceived by humans) suggests that some areas of the tongue could be differentiated in terms of local taste response.(Courtesy of Dr. Werner Meinel.)

PSYCHOSENSORY RESPONSES

The most spectacular response elicited by tasting, the gusto-facial reflex, has been observed in human babies[19] (Fig. 3), as well as newborn non-human primates.[20] Neonates react in stereotyped ways, either rejecting bitter solutions with a typically arched form of the mouth or by accepting sugar solutions by sucking with a relaxed facial expression. As Steiner[19] noted, this display, often accompanied by a slight smile, looks like an expression of satisfaction. During behavioral development,[21] this response is generally reinforced by parental smiles, a nonverbal form of communication that contributes to the pleasure of food perception and its variation.

In behavioral terms, the affective value (likes or dislikes) attributed to food tastes can be considered a sensory reward[22] that eventually involves the release of opioid substances.[23] This process is modulated during different phases following ingestion: 1. Sensory-specific satiety is a rapid variation of the pleasantness of the taste of one food item that occurs before any gastric satiation can be felt.[24] In macaques, extreme specificity toward one food type corresponds to inhibitory responses of single neurons of the orbito-frontal cortex[25] that do not occur for other food types. 2. Alliesthesia is a middle-term variation of the affective value of food taste that results from stimulation of duodenal chemoreceptors by the food ingested.[26] This mechanism is less specific than the previous one because various alimentary tastes-cum-odors are affected simultaneously.[27] 3. The long-term response of hunger versus satiety, which is related to a decrease in blood glucose,[28] also influences food pleasantness.[29] All these mechanisms affecting the sensory reward associated with food taste are necessary. Without the short-term sensory-specific response that can stop intake, one could eat too much before the blood

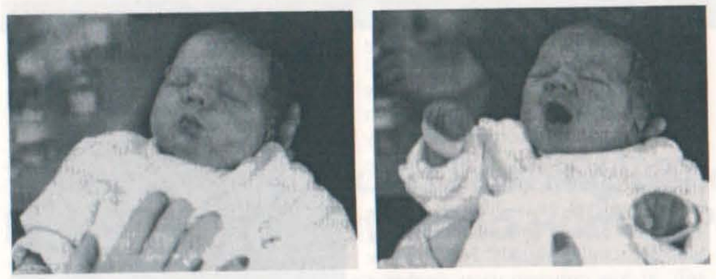


Figure 3. Illustration of the gusto-facial reflex of a young baby. A relaxed face (left) follows tongue contact with a sugar solution, whereas contact with quinine produces a strong rejection reflex (right). These responses imply separated projections of some best-responding taste fibers towards basal brain structures. (Courtesy of Professor Matty Chiva.)

glucose reached a normal level,[30] or drink excessively before osmoreceptor signals prevent a dangerous dilution of internal fluids.[31]

In addition to genetically determined mechanisms, learning processes also influence the perception of food taste. One of the most striking interactions between physiology and behavior is conditioned taste aversion. Garcia and Koelling[32] showed that aversion to a particular taste can be artificially induced by a single experience of nausea following ingestion. This efficient conditioning process can be viewed as an emergency system for short-circuiting the successive and partly overlapping mechanisms that regulate food intake in mammals. Conversely, a progressive change in food preference was observed in rats that initially consumed a highly palatable but nutritionally poor diet: when distasteful but nutritious food was made available, the animals learned to prefer it after only a few days.[33]

Such learning processes are prevalent during the exploratory phase in development.[34] Young children, after watching a respected older child eat a particular dish, may subsequently crave that food, although they did not initially prefer it. In adults, a similar social response occurs independently of the nutritional or health virtues of the products ingested. In several societies, this could be called the beer-and-tobacco syndrome. Although embedded in culture, humans' acquisition of food likes or dislikes is comparable to conditioned taste responses in other mammals. Being part of a social group can be a reward; the feeling of exclusion can raise as much aversion as the nausea provoked by noxious food.

INVESTIGATING PRIMATE TASTE

Methods used in the study of primate taste perception must be adapted to the recent advances in the field of taste physiology mentioned earlier. In addition, all results need to be discussed in the context of integrative psychosensory processes.

In nonhuman primates, taste thresholds, as well as profiles of suprathreshold ingestive responses, can be measured by a standard behavioral method, the two-bottle test adapted for statistical analysis.[35] In this test, the tastant solution and tap water are presented simultaneously to a monkey. Consumption of both liquids is measured, after a delay to determine at what concentration level the monkey shows preference or avoidance of the tastant. Although it has been found that the behavioral thresholds of some primate species are quite similar to thresholds obtained by directly recording signals on a peripheral taste nerve,[36] these results must be carefully interpreted because the test provides information on both taste discrimination and preference.

In contrast, experiments on humans have been focused on discriminative ability, including recognition of the taste of various substances. Tastants such as glucose, fructose, sucrose, sodium chloride, citric and oxalic acids, quinine hydrochloride, thiourea, and tannins were given to subjects who knew what substances were available, but did not know which one they were being asked to recognize. The different substances were presented at random, starting with the weakest solution and progressing in order of increasing concentration. Statistical tests (χ^2) confirmed significant differences between populations.[37,38]

Several studies of taste thresholds in humans have been based on the ability to differentiate plain water from a solution of the taste carrier. These tests have aimed at detecting the onset of the taste signal, rather than at determining the concentration necessary for unambiguous recognition involving the overall taste signal. We did not use this detection threshold, which is of minor importance in feeding behavior because cognitive aspects associated with food preferences require identifying the taste signal.

Although embedded in culture, humans' acquisition of food likes or dislikes is comparable to conditioned taste responses in other mammals.

SUGARS AND NONHUMAN PRIMATES

Most nonhuman primates include fruits in their diet. The form and function of the digestive systems of several species have been shaped in accordance with the evolution of fruit-bearing plants since the Mesozoic.[39] Although fruit composition varies across plant species and in relation to ripening, fruits generally include soluble forms of sugars, mainly fructose, glucose, and sucrose. The proportions of these sugars in fruits eaten by wild primates have been studied, especially in Sri Lanka, Gabon, and French Guiana, in relation to seasonal availability and interspecific differences in food choice.[40,41] Total soluble sugars generally vary between 25% and 70%

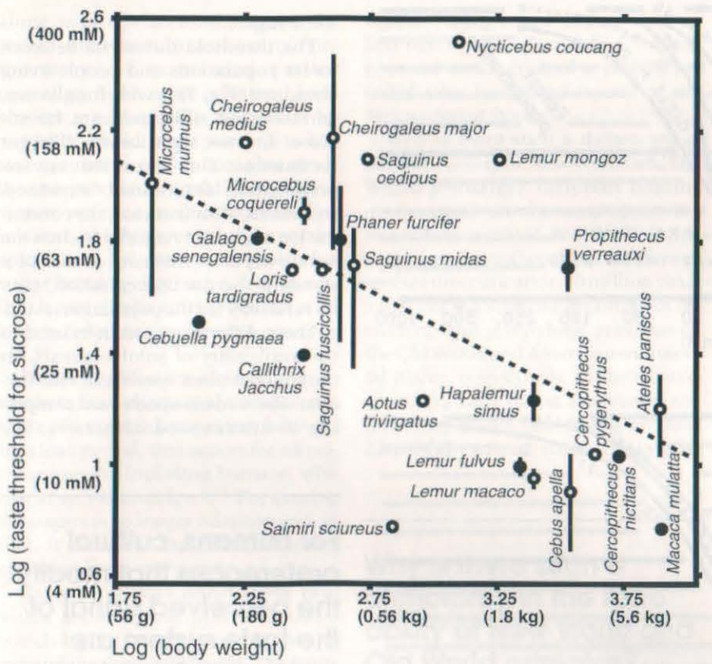


Figure 4. Correlation between the taste threshold for sucrose and the body weight of primate species. Primates having a diet that includes large amounts of leaves or gums and less than 50% fruit are shown by solid circles; open circles designate more frugivorous species. The function is exponential, as are all allometric relationships, and the decimal log-log transformation of the data results in a linear regression line (broken line; slope = -0.49) showing the overall trend. Large deviations from this baseline, such as those shown by the slow loris, *Nycticebus coucang*, and the squirrel monkey, *Saimiri sciureus*, most likely reflect peculiar dietary adaptations.

of the dry weight of ripe fleshy fruits (that is, about 60 to 180 grams per liter in the juice), although proportions as low as 1.5 % have been found in some wild fig species.

The thresholds for sucrose, which are known for 33 nonhuman primate species,[42] vary between 6 and 330 millimoles (mM), which corresponds to 2 to 113 grams per liter. The thresholds for fructose, measured for a limited number of primates, appear to vary within similar limits across species. Because these "behavioral thresholds" are the minimum concentrations that a fruit can have and still remain attractive to primates, ripe fruits have a sugar content that can actually be tasted and that, for most primate species, produce a sensory reward.

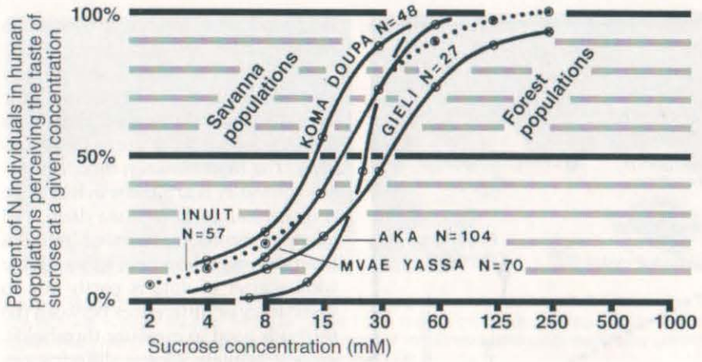
Surprisingly, the threshold for sucrose is correlated with species body mass (Fig. 4). We initially assumed that taste ability is an adaptive response to the composition of foods available in the environment.[43] But this sensory adaptation could also be linked to body size, for the size and shape of most body parts, including the brain[44] and gut,[45] are related to weight and skin area. Indeed, a wide area of the lingual mucosa in large animals may increase taste performance. The correlation between body weight and taste thresholds for sucrose, shown in Figure 4 by the logarithmic plot of primate species, is significant in a linear regression. Thus, the larger the species, the better taste acuity (i.e. low threshold). We found a similar correlation between taste ability and body mass for fructose, although fewer data were available regarding thresholds. We interpret these relationships as reflecting the importance of taste acuity to improve foraging efficiency. Because primates with large bodies perceive a wide range of sugar concentrations as palatable, they use a wide array of foodstuffs, including some with a relatively low sugar content, to meet their energy requirements.[46]

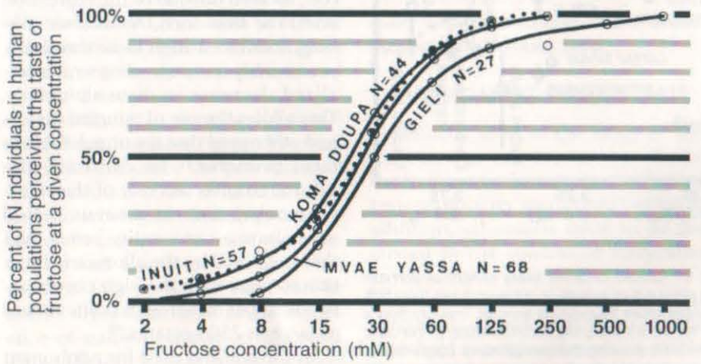
The species shown in Figure 4 may most often eat fruits (open circles) or may also include in their diet large amounts of leaves or gums (solid circles). The limit between these categories obviously is arbitrary. In fact there is a continuum in primate diets. The adaptive trends are revealed by shifts from the regression line, although the wide scatter of data is partly due to inaccuracy or differences between the methods used to measure thresholds. Among primate species differing noticeably from the common pattern (i.e., located outside of the regression line), the slow loris, *Nycticebus coucang*, exhibits a high taste threshold, presumably corresponding to a generalized decrease in taste sensitivity. This allows the use of pungent insects and other prey that are unpalatable to most primates.[47] In contrast, the eclectic frugivorous diet of the squirrel monkey, *Saimiri sciureus*, would necessitate a taste acuity better than that predicted by the allometric function to cope with the high energy expenditure of foraging in home ranges as large as 250 hectares.[48]

In the method used for nonhuman primates, taste threshold is the limit above which a sensory reward can be associated with sugar discrimination. However, the perceived intensity above threshold must obviously be of great significance in terms of sensory pleasure if it is to sustain a specific diet. For instance, the ingestive response of several tamarins increases more rapidly with fructose concentration than that of marmosets, even though these closely related species have similar taste thresholds.[49,50] The difference corresponds to distinct dietary tendencies: tamarins feed mainly on sweet fruits, whereas marmosets, such as *Cebuella pygmaea*, most often eat tree exudates, especially gums that contain few soluble sugars.

SUGARS AND HUMAN POPULATIONS

Among the human populations investigated so far, taste thresholds for sugars accord well with values predicted by the primate scaling model; i.e. those of a primate with a large body mass and an omnivorous feeding





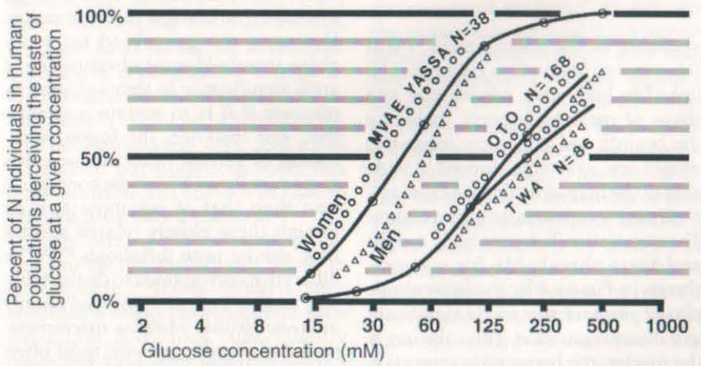


Figure 5. Taste thresholds for sugars in different populations living inside and outside the African rain forest, and in one Inuit population (dotted lines). Each of the curves shows, for a given population or group of populations, the cumulative percentages of people able to recognize the taste of a solution at a given concentration (logarithmic scale on abscissa) during standardized tests. The Aka and Gieli Pygmies of the Central African Republic, as well as the Oto and Twa of Zaire and the Mvae and Yassa of south Cameroon—all forest populations—have a significantly higher threshold for sucrose and glucose than do the populations of north Cameroon, the Koma, and Doupa. The difference between men and women in glucose taste sensitivity is not significant among Pygmies, but is significant ($P < 0.05$) among Mvae and Yassa.

strategy. Nevertheless, differences have been observed between human populations living at a subsistence level in tropical rain forests and populations living in other environments, with respect to taste thresholds for some sugars.[37]

The threshold difference between forest populations and people living elsewhere (Fig. 5) is wide for glucose, narrower but still significant for sucrose, and not significantly different for fructose. This means that any experimentally determined "sweetness equivalent," (for instance, the concentration of glucose required to elicit the same sweetness intensity as that of a standard sucrose concentration) may be valid only for the population tested.

These differences can be related to the availability of soluble sugars, in the fruits of plant species. In rain forests, where many species are competing to attract seed dispersers, the sugar concentration in fruits can be high. Accordingly, it is not surprising that Pygmies have a relatively poor taste acuity (median threshold for glucose at 200 mM) as compared with populations living outside the African tropical forest (median threshold at 50 mM). Efficiency in finding energy in fruits can be increased by taste sensitivity in savanna populations facing an environment in which low plant diversity results in fruits having lower sugar content than do forest species.[51]

Obviously, additional data would be needed to support this neo-Darwinian interpretation; selective pressure

For humans, cultural preferences that modify the perceived signal of the taste system are even more important. For instance, the Pygmies value honey, despite their low taste sensitivity for sugar because climbing a tree to collect honeycombs among furious wild bees is risky, making honey a precious gift.

alone may not account for the observed differences in taste acuity. Furthermore, as mentioned earlier regarding nonhuman primates, food choices are essentially influenced by suprathreshold perception. For humans, cultural preferences that modify the perceived signal of the taste system are even more important. For instance, the Pygmies value honey, despite their low taste sensitivity for sugar because climbing a tree to collect honeycombs among furious wild bees is risky, making honey a precious gift.[52]

In affluent Western societies, supermarkets have eliminated the seasonal cycle of an abundant period followed by a lean period, that occurs for all primate species, including humans, who live at subsistence level.[53] The craving for sugars is no longer adaptive and, in fact, it increases the risk of diseases resulting from overweight.

Taste sensitivity nonetheless provides a biological platform upon which higher cognitive aspects act to expand the perceived world. The fruits of the rain forest eaten by Pygmies have a sugar content 10 to 50 times higher than that of the weakest sugar solution perceived. Consuming fruits and appreciating their taste is still in the field of biological phenomena. Furthermore, several other interactions between sweet taste and the environment need examination.

SWEET TASTE AND EVOLUTIONARY INTERACTIONS

Since saccharin was fortuitously synthesized in 1879, several nonsugar products that taste extremely sweet have been found, even among natural substances. Their chemical structure is totally different from that of sugars[54]; for instance, monellin, the natural sweet compound found in the red berries of a liana of the African rain forest, *Dioscoreophyllum cumminsii*, is a protein that as perceived by humans, tastes 100,000 times sweeter than sucrose at equivalent molar concentration. But monellin and other "natural sweeteners" are tasted most keenly by Old World primates, including humans; New World primates are not able to perceive the taste of such sweet solutions. This difference in tasting ability is presently under investigation, using a new protein that we first described as "pentadin,"[55] which is found in the fruit of a plant (*Pentadiplandra brazzeana)* typical of the African forest flora.

Why is there such a dichotomy in the taste ability of New World and Old World primates? Different binding mechanisms on chemoreceptors are most likely involved. Protein evolution in taste receptors would have followed species diversification 30 million years ago, after the separate evolution of catarrhine and platyrrhine primates on the Old World and American continental plates, respectively. In their corresponding rain forest environments, flowering plants competing for seed dispersal evolved fruits containing large amounts of sugars; the more sugar, the more efficient their dispersal by consumers. Owing to the strong taste of "sweet proteins" at low concentration, the energy plants invest in their synthesis is low compared with that they invest in synthesizing sugar. As a result, genes coding for the fortuitous emergence of proteins with tastes mimicking that of sugars would be selected for. Primates feeding on these fruits are "tricked" by the plant species: They work as seed dispersers without receiving any energy in return (although they do obtain a sensory reward). As in Batesian mimicry, such interaction is made possible by the widespread occurrence in rain forests of fruits with true sugars[56] that serve as a model.

Why is there such a dichotomy in the taste ability of New World and Old World primates? Different binding mechanisms on chemoreceptors are most likely involved.

This coevolution between primates and plants that contain nonsugar sweeteners has been observed only in Africa. In America, where no such substance has been found so far, one might still expect a similar coevolutionary process to have occurred. Just as present African sweeteners are tasteless to American primates, sugar mimics of American fruits might be tasteless to Old World primates, including *Homo sapiens*. Such hypothetical substances, dubbed "tasteless sweeteners,"[51] have yet to be discovered in the New World.

STARCHES, FATS, AMINO ACIDS, AND PROTEINS

Taste sampling of soluble sugars allows high energy intake through immediate preference, but this is not true with other high-calorie foodstuffs. Several nutritious foods, such as tubers, grains, nuts, and, indeed, most plant parts containing starch or fat, have little taste, even though they are staple foods for human populations. Similarly, gums and other plant exudates containing long-chain carbohydrates, which are consumed by several primate species and considered to be staple foods for lemur ancestors,[57] are characterized by their peculiar jelly-like texture, rather than by a typical taste. Current investigations indicate that tactiles cues (fat viscosity or the floury scratch of starch in the mouth) are important organoleptic characteristics of these foodstuffs.[58]

The preference for fat has been primarily investigated among humans, for whom obesity and associated diseases are of major concern. The hedonic value of oils, like that of sugars, varies with hunger and satiety.[27] The solid versus the liquid form of fat also influences preferences.[59] It is not clearly understood, in all instances, whether a proper taste signal helps to identify starch and fat; the preference of newborn rats for starch[60] could be based on either tactile cues or a typical taste response. Similarly, some primate species show various responses to starchy substances,[61] so that the possibility of differential abilities to taste polymerized carbohydrates cannot be ruled out.

As compared to the clear-cut responses to soluble sugars, the apparently imperfect taste response to these highly nutritious compounds could be related to the fact that the radiation of

flowering plants is relatively recent. Whereas sugars, always present in plant metabolic pathways, may have been concentrated in fruits of the early angiosperms, fatty fruits seem to be the result of a more recent and sophisticated evolutionary process. In this case, the trend toward reduction in the size of the fruits is compensated for by their provision of greater energy intake: A fatty, thin aril provides more energy than does a sweet pulp.[62] In consequence, the seed of such fruits is dispersed by a wide range of frugivorous animals.

Perception of substances with high nutritional importance, such as amino acids and proteins, is even more puzzling. There is no simple relationship between the role of essential amino-acids and their palatability. For instance, purified D-tryptophan is rejected by Cebidae and one lemur so far tested, but appears palatable to some Callithrichidae and Cercopithecidae.[63] To humans, some amino acids or peptides taste sweet, whereas others taste bitter.[64] Protein that mimics sugars falls in the category of substances that taste different to different primates according to the recency of their evolutionary radiations.

Primates meet their protein requirements by eating leaves, seeds, or animal matter. The protein intake of leaf-eating primates, such as *Presbytis* spp., is above requirements, decreasing slightly when fruits are mixed in large quantity with leaves.[65] For such species, what is tasted may not be the major factor determining food choices; instead, the long-term post-ingestive effects common to all vertebrates can efficiently regulate feeding behavior. In contrast, when capuchin monkeys or chimpanzees crack nuts to extract the seeds, an act necessitating high skill and energy expenditure,[66,67] they may expect an immediate sensory reward. Whether starch, fat, and protein stored in seeds elicit specific taste signals is still being debated. However, perceptive factors, including odorant and tactile cues, certainly contribute to sensory pleasure. Chimpanzees sharing animal prey and slowly eating it in small pieces[68] may combine taste pleasure with social contact.

"Umami," the taste of glutamic acid and derivatives (monosodium glutamate), which has been described as the fifth taste,[69] is particularly appreciated by the Japanese. It is typical of crab flesh, and may also contribute to the taste of some fruit pulps. As we have already emphasized, there is no evidence that a limited number of basic tastes exists. We have to consider each amino acid as separately eliciting a singular "taste signature," genetically determined but eventually modified by socially acquired representations.

SALT PERCEPTION

The ability of vertebrates to taste sodium chloride and the positive response to this taste by several species have been considered as adaptive features that prevent sodium deficiency.[30] However, mineral deficiencies are unlikely to occur among wild primates, especially in forest environments where available foods provide higher dietary supplies than estimated requirements. This was shown at Panama, Sri Lanka, and Gabon, with respect to sodium and some other essential minerals in the foods of various primate species.[40,70]

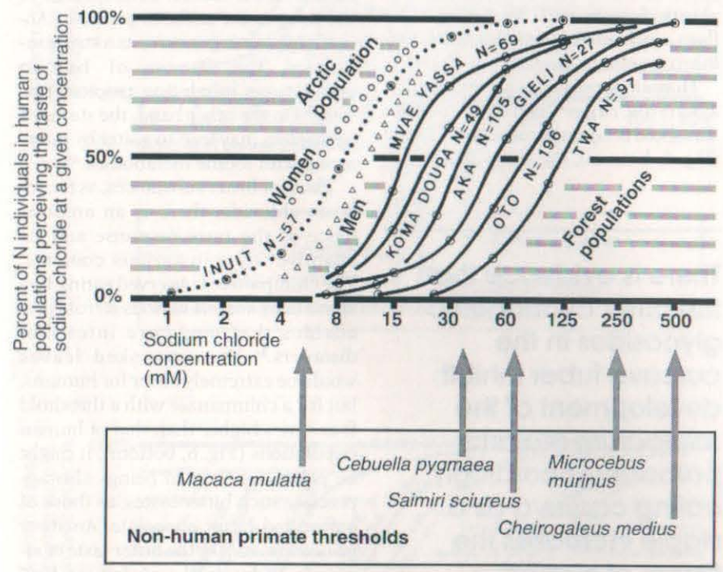
The extreme sensitivity to sodium observed in the Inuit population (median threshold at 8 mM) can provide a selective advantage. The high Inuit sensitivity is associated with an aversion to too much salt, which traditionally is considered to be dangerous.

Although generally not lacking in the diet, sodium chloride is present at low concentration in most plant parts (less than 0.5% of the dry weight, or below 20 mM concentration). Most primates, which have thresholds ranging between 5 mM and 500 mM,[63] cannot perceive the resulting salty taste (Fig. 6, top). However, the large petioles of *Musanga cecropioides*, which chimpanzees in Gabon carefully peel off and crunch, have a sodium chloride content reaching 1.34% of the dry weight,[70] a salt concentration that is above the threshold of some primate species.

Soil eating is common in primates,[40,65,71] giving rise to the question of whether geophagy plays a role in mineral nutrition. Clay and other phyllitous soil materials that primates eat can also work as adsorbent of tannins from the stomach contents (i.e. molecules are retained on the particles of clay). This beneficial effect is the most likely explanation for geophagy during periods of intense feeding on mature leaves that contain digestibility reducers such as tannins.[72] Indeed, Johns and Duquette[73] measured the amount of tannins bound with clay, demonstrating that adsorption is efficient enough to allow quiet digestion.

Like nonhuman primates, humans living in tropical forests are unlikely to face sodium deficiency if they rely on plant foods. This might explain the relatively low sodium sensitivity of Pygmies,[37] some populations of which have a median threshold of 100 mM (Fig. 6, top). Conversely, the extreme sensitivity to sodium observed in the Inuit population (median threshold at 8 mM)[37] can provide a selective advantage. The high Inuit sensitivity is associated with an aversion to too much salt, which traditionally is considered to be dangerous.[74] As far in the past as 2000 BC, the Inuit population of the west coast of Greenland has concentrated all its food-gathering and hunting activities within a narrow coastal fringe. The staple that consistently has provided most calories in the Inuit diet is seal meat and fat, presently derived from the ringed seal (*Pusa hispida*). Seal meat is always boiled in water, and without much salt. The traditional life of hunter-gatherers, by now integrated into a modern socio-economic context, involves a diet having a particularly high protein content.[1]

As a result of the Inuit diet, drinking large amounts of water is physiologically necessary to prevent urea from accumulating in the bloodstream. Early explorers of Greenland noticed that all eskimo populations drank remarkably great quantities of fresh water. Draper[75] showed that this is an important feedback mechanism that is necessary for the elimination of excess urea. A diet that includes a high amount of protein induces proportionally high dietary-induced thermogenesis (DIT); which leads to greater meat consumption to balance calorie input and output.[76] The increase in urea results in consumption of large amounts of water. The use of melted ice from small icebergs that have been in contact with salty water, which increases the risk of sodium excess, needs accurate salt perception at low temperature.[77] Although the risk of associated cardiovascular diseases mostly concerns adults, it is a selective pressure favoring genes that code for low taste threshold. Children's survival traditionally depended on the hunting capacity of their fathers.[43]



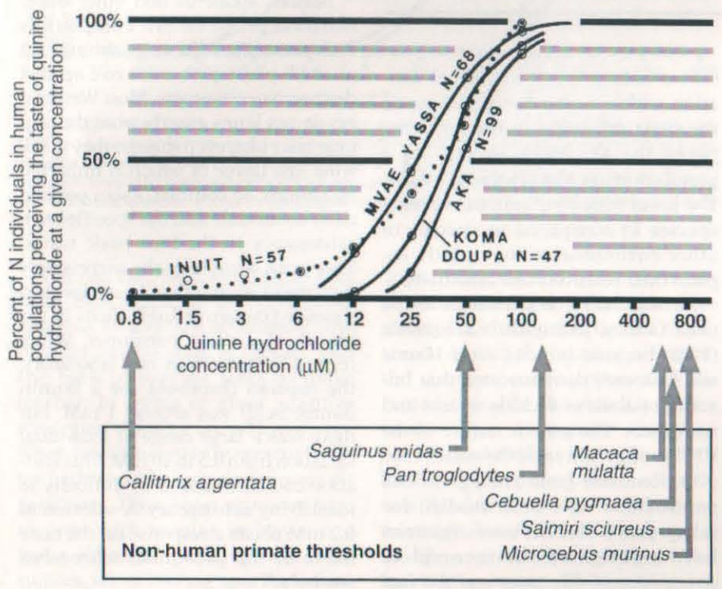


Figure 6. Taste thresholds for sodium chloride (top), and quinine hydrochloride (bottom) in different human populations. The large difference between Inuit and other populations in sodium chloride sensitivity is significant ($P < 0.001$). Among the Inuit, women can perceive lower sodium chloride concentrations than men can ($P < 0.05$). The Aka Pygmies have a significantly higher threshold for quinine than do the other populations tested (P 0.05). The thresholds of nonhuman primates species (preference thresholds, determined with the two-bottle test) are shown on scales that are similar to those for human populations.

TASTE AVERSION AND FOOD TOXICITY

Bitter plant substances such as several alkaloids, as well as astringent compounds (mostly tannins), terpenes, saponins, and strong acids elicit a vigorous rejection — initially, a "gusto-facial reflex"[20] — that obviously is adaptive, for many of these products are toxic. It is assumed that the ecological function of these potentially toxic substances is to defend the plant against harmful consumers.[78] However, toxic species do not necessarily elicit a warning taste signal that humans can identify. A lethal alkaloid such as the dioscine of *Dioscorea dumetorum* is almost tasteless, but this wild yam growing at the edge of the African tropical forest is as dangerous as some *Amanita* spp. mushrooms growing in temperate forests. In most instances, however, a behavioral response, neophobia,[79] prevents the ingestion of large quantities of a novel food, and thus minimizes the danger of plant toxicity. The ingestion of a few bites by animals sampling their food is sufficient to induce post-

ingestive symptoms that lead to taste aversion.

Glander's[80] review of the effect of such substances on primate food choice shows that plant parts are frequently selected on the basis of low alkaloid or tannin content. But this is not a general rule; the concentration and toxicity of these substances can vary widely in different types of environments. In the Gabon rain forest, for example, where 14% of the 382 plant species tested reacted positively to the alkaloid test, the chimpanzee includes in its diet a similar proportion (15%) of plants likely to have a high alkaloid content.[4] Accordingly, because chimps have no particular detoxification system, most alkaloids in this environment can be compared to caffeine in their weak toxic effect. Furthermore, observation of chimpanzees in a montane forest "curing themselves" with a bitter plant species, *Vernonia amygdalina*, which usually is discarded by healthy individuals,[81] provides evidence that the aversive response to alkaloids can be reversed. Whether this behavior qualifies as a medicinal practice based on cognition or whether it reflects a conditioned taste response can be better understood in light of recent data on primates' perception of bitter substances.

One may wonder why taste thresholds for quinine vary so widely from 0.8 to 800 micromoles per liter (μM), among nonhuman primates (Fig. 6, bottom). In direct contrast to what was observed for sugars, no relationship could be found between the taste sensitivity to quinine and the body weight of different species.[42] This should not surprise us; quinine is not a nutrient, the need for which would increase with body weight. A wide range in sensitivity may reflect the adaptations of different primate species to different nutritional environments, as exemplified by the two marmosets, *Callithrix argentata*, living on white-sand riverine forests, and *Cebuella pygmaea*, inhabiting the interior of the rain forest.[50] Both species feed mainly on the gum exuded by a tree bark after they have gouged it with their incisors. These primates are in contact with bark substances evolved by tree species as chemical defenses (for instance, quinine is a chemical substance in cinchona bark). However, because of the different environments these marmosets live in, the alkaloid content and toxicity of the bark is likely to vary. Contrary to rain forests where, as for chimpanzees in Africa, there is little risk in eating bitter plants, forests with less diversified flora, such as that inhabited by *Callithrix argentata*, present a high risk.[4]

Human populations are grouped in a narrow range having a median threshold for quinine of around 25 μM (Fig. 6, bottom); the steep slope of all curves indicates low individual variation within a population. However, the slight difference in threshold between the Aka Pygmies and other populations is significant ($P<0.05$). The lower toxicity of rain forest plant species as compared to species in other environments may partly explain their relatively low sensitivity.

There is evidence that the bitter cyanogenic glycosides in the cassava tuber inhibit development of the *falciparum* malaria parasite. Accordingly, eating cassava as a staple increases the fitness of human populations inhabiting tropical forests.

Among the bitter chemicals in the urea family, phenylthiocarbamide (PTC) became famous after Harris and Kalmus[82] demonstrated that human populations include tasters and nontasters. The genetic nature of the PTC tasting ability and the occurrence of a dominant gene among various populations have been studied for many years. Recent investigations have highlighted the incomplete dominance of one gene and the fact that some others play a minor role.[83] Why has such a polymorphism been maintained in a mammalian species confronted with the noxious, bitter substances of its environment? On one hand, there is evidence that the bitter cyanogenic glycosides in the cassava tuber inhibit development of the *falciparum* malaria parasite. Accordingly, eating cassava as a staple increases the fitness of human populations inhabiting tropical forests.[84] On the other hand, the status of nontasters may lead to goiter by interfering with iodine metabolism.[85]

Thus for bitter substances, as for sodium chloride, there is an ambivalence of the taste response and its adaptive value in various contexts. The chimpanzees observed eating *Vernonia* leaves ingest various steroid glucosides that may cure intestinal disorders.[86] The uncooked leaves would be extremely bitter for humans, but for a chimpanzee with a threshold four times higher than that of human populations (Fig. 6, bottom), it might be palatable. Human beings also appreciate such bitter tastes, as those of coffee and bitter chocolate. Amateur gastronomers like the bitter taste of almonds, endive, and curly lettuce. Several tropical forest populations also prefer bitter cassava to sweet cultivars.[87]

Besides alkaloids and other bitter substances, phenolic compounds such as tannins, which are common in plants,[88] play a protective role against destructive consumers. Most Westerners do not know exactly what the tannins taste like, even though they drink wine, the flavor of which is imparted by tannins. In contrast, Asian populations commonly add the specific term astringency to the four basic tastes. This word designates the surprisingly distasteful feeling that an unripe persimmon (*Diospyros kaki*) elicits in the mouth of a naive consumer. When testing volunteers in our laboratory, the median threshold for a tannin (tannic acid) was around 1 mM, but there was a large range of individual variation from 0.3 to 10 mM. This variation could be caused by difficulty in identifying astringency. A solution at 0.2 mM elicits a response on the taste nerve of the prosimian *Microcebus murinus*.[89]

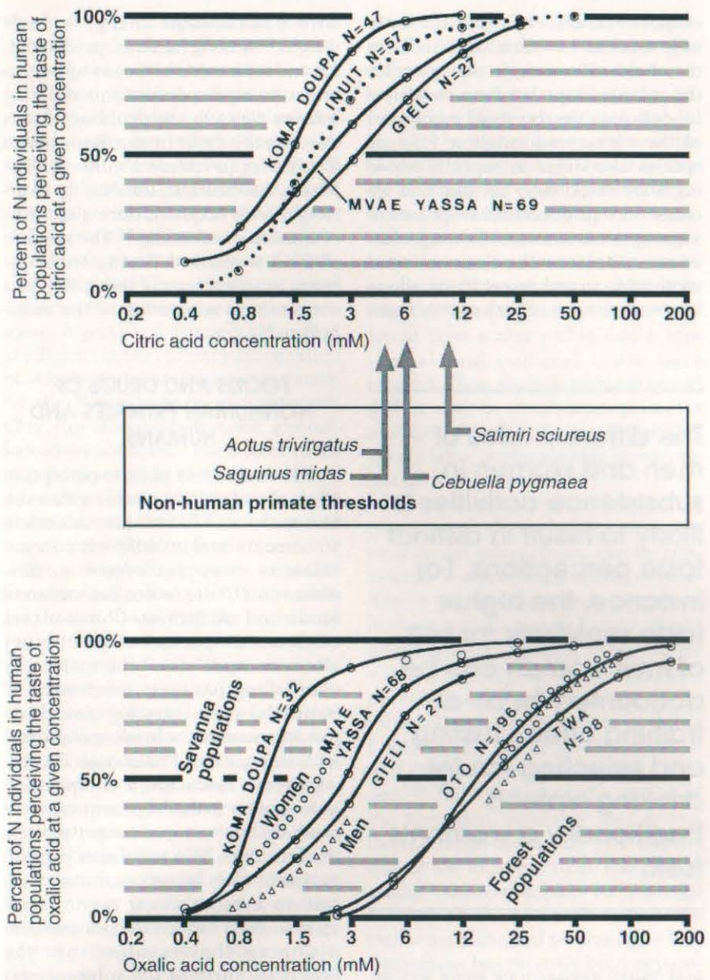


Figure 7. Taste thresholds for citric acid (top) and oxalic acid (bottom) in different human populations and nonhuman primate species. Recognition thresholds are indicated for human populations, whereas preference thresholds (two-bottle test) are shown for nonhuman primates. Differences between forest and nonforest populations are significant for both acids ($P<0.001$). Among Mvae and Yassa populations, women have a significantly lower threshold for oxalic acid than do men ($P<0.05$).

Tannins can bind strongly to proteins. Even in ancient times this property was well-known to tanners, who brought animal skins in contact with the bark of various trees to make leather. In terms of plant adaptive strategies, tannins are efficient only when large amounts are present to deter herbivores by reducing protein digestibility. Thus, most primates have to cope with tannins in leaves and fruits, although tolerance to these substances varies among species.[90] Condensed tannins and hence their unpleasant taste, tend to decline as fruit matures, a change that occurs simultaneously with the increase of sugars; the taste response is necessarily directed towards the resulting mixtures. For instance, *Callithrix jacchus* and *Callimico goeldii*, which have similar perceptions of fructose,[50] tolerate tannin and fructose mixtures, but reject them when the tannin content reaches 4% of the fructose content. Thus, the more sugar in the mixture, the more tannin is tolerated.

ADAPTATION TO ACIDS

A strong acid taste is generally deterrent. The mild reaction of babies to an acid taste, a gusto-facial reflex consisting of lip-pursing,[19] obviously is a result of the weak concentration of the acid used in this test. Strong acids elicit a painful trigeminal response;[91] Chili and hot pepper cause this response to merge with all other parameters of the taste signal. Owing to the risk of excessive variation of the pH of the *milieu interne*, as for instance, when a lemon or lime (pH as low as 2) is ingested, the adaptive nature of the displeasure associated with extreme sourness can be inferred. Taste thresholds for citric acid among the nonhuman primates so far tested do not differ widely from those of human populations whose median thresholds (Fig. 7, top) lie between 1.5 and 4 mM. Oxalic acid present in several plant species (such as the leaves of sorrel, *Rumex acetosa*) elicits extremely diverse responses in human populations (Fig. 7, bottom), the median threshold ranging from 1 to 20 mM.

One primate species, the night monkey (*Aotus trivirgatus*), which includes sour fruits in its diet, shows a preference for citric acid solutions at low concentration, whereas all other primates tested avoid sour solutions.[92] A more subtle difference has been observed between sympatric primate species of Sumatra.[93] Whereas most fruits eaten by gibbons (*Hylobates lar*) are extremely acid, having a pH as low as 1.5, orangutans (*Pongo pygmaeus*) and macaques (*Macaca fascicularis*) eat larger proportion of fruits with a pH between 4 and 5. Langurs (*Presbytis thomasi*), which eat more fruits with a pH >5, avoid the most acidic fruits. In this species, a decrease in pH could destroy the symbiotic microorganisms that allow fermentation in the forestomach, which is a characteristic of all leaf-monkeys.

A decrease in acid content accompanies sugar accumulation in ripening fruits. Because the sourness of a mixture decreases when sugar is added,[94] the ripening of fruit enhances its palatability, making the pulp as at-

tractive to wild primates as soft drinks are to children. The pleasantness of a mildly sour taste may help meet requirements for ascorbic acid (vitamin C). However, considering the ascorbic acid content of leaves and fruits in a tropical forest,[95] wild primates do not risk being deficient.

FEEDING STRATEGIES AND TASTE PERCEPTION

Primate diets can be understood in terms of feeding strategies, the various ways used to cope with potential foods and their seasonal variation.[53] Whereas some species tend to supplement a diet of animal matter with fruits, others are mainly frugivorous. Still others use leafy materials as a major energy source. These materials have very different nutrient contents,[96] especially in terms of sugars.

The preference for soluble sugars, which is observed in all primates, allows an efficient quest for foods having a high energy content. Different strategies can be maintained through differently perceived intensities of taste stimuli. For instance, macaques and capuchins need to spend great amounts of energy to find scattered resources such as sweet fruits and insects; in turn, these resources provide a high energy return. Conversely, species such as langurs and howlers eat the foliage and unripe fruits of common plant species, which give a low energy return. However, this strategy necessitates a lower energy investment than required of macaques and capuchins. To account for these opposite strategies, which imply a grade of intermediate types, a model in which taste perception plays a major role has been proposed.[4] According to this model, species with the highest taste sensitivity for sugars and other soluble nutrients tend to improve foraging efficiency, whereas species with low taste responsiveness mostly rely on the long-term satiating effect of low calorie foods.

Taste sensitivity for sugars tends to increase with a species' body mass, as illustrated in Figure 4. Furthermore, most species that depart from this pattern have specialized feeding strategies, tending toward either the high energy input and output of the best tasters, or the low energy input and output of others. Phylogenetic inertia may account for some similitudes in thresholds. However, in our quest for the relationships between taste and food choices, the threshold is only part of the relevant information. Primate species also differ in suprathreshold ingestive responses.[50] A marked increase in suprathreshold responses to sugar concentrations, reflecting a fast increase in pleasantness, may enhance motivation to seek sweet fruits, allowing for strategies of high energy input and output even among small species.

The different roles of men and women in subsistence activities is likely to result in distinct taste perceptions. For instance, the higher taste sensitivity for salt of Inuit women can be accounted for by a training effect: tasting and selecting ice for drinking water is traditionally a woman's task.

Although median taste thresholds in human populations fit the model, they obviously are not sufficient to account for most differences in food choices without also addressing the extremely diversified cultural considerations. The risks associated with obesity are a major concern in the present-day Western world, where food habits are no longer determined by seasonal variation, including a lean period. For wild primates and populations living at subsistence level, fat accumulation is an adaptive response to coping with uncertainty in food supply.[97] In the lesser mouse lemur, *Microcebus murinus*, as well as in other Cheirogalidae, there is a seasonal variation in sugar preference concomitant with a remarkable change in body weight.[35] Among humans, psychological and sociocultural factors appear to be extremely important in modulating sensory pleasure and deciding what is the desirable body image. Body image also varies in different cultures. The Massa, for example, idealize the overweight body acquired during sessions of intense overfeeding.[98] The amount of food consumed during such sessions is so enormous that there is a concomitant adaptation of the metabolism.[99]

FOODS AND DRUGS OF NONHUMAN PRIMATES AND HUMANS

The dual aspect of taste perception of plant and animal products that can be beneficial or harmful in various environments and at different concentrations may introduce a new dimension to the recent discussion of foods and medicines. Chimpanzees can learn the positive effect of bitter alkaloids and "cure" themselves by controlling parasitic infection.[81,100] Similarly, when ingesting clay, chimpanzees prevent the binding of protein with leaf tannins. The clay gorillas eat with toxic foods has a composition quite similar to that of pharmaceutical products known to reduce gastrointestinal troubles.[101] A satisfactory explanation of such behaviors, rather than rest on a hypothetical cognitive response, must include the positive conditioning that results from the beneficial effect of the substance ingested, as demonstrated in rats with nutrients.[102]

A rigid classification of natural products into two categories, foods and medicines, reflects present-day Western concepts and the approach of commercial enterprises such as grocery stores and pharmacies. This is a change from traditional categories whereby different collective representations were used for drugs and foods.[103] As Johns[104] has suggested, the origin of medicine shows that human perception, cognition, and behavior are related to plant chemicals, and reflect both cultural responses and biological trends.

Early hominids evolved in a changing environment in which nutrients and toxins were mixed in most potential foods. An extrapolation from the present food habits of hunter-gatherers and the rare information about fossil food plants in prehistoric sites provides evidence of a diet that included animal foods, but in large degree was based on plant carbohydrates.[105] Among these resources, acorns necessitated the elimination of tannins, not only to improve their taste, but to prevent binding with protein, and digestive difficulty. Clay, which, as noted earlier, chimpanzees and other primates ingest to eliminate leaf tannins, is efficient in the culinary preparation of acorns and was used, for instance, by the Pomo Indians of California. Clay can also detoxify toxic glycoalkaloids in potatoes.[73] Food technology may have been one of the first cultural advances of hominids, though some chemical properties of plants would have been difficult to overcome.

Physiological responses to toxins are extremely diverse.[104] They allow for the use of, and even the preference for, several plant species that would be poisonous if eaten in large amounts. In natural environments, alcohol is exclusively present in sweet fruits that have fallen on the ground and fermented. Goodall,[106] quoting Temerlin, describes a chimpanzee "laughing... and getting high" after eating completely rotten fruits. Most human populations generally use alcoholic beverages in convivial or festive contexts.[2] Other products used in such contexts might be more noxious if ingested in large quantity. For example, the Inuit enjoy consuming small pieces of shark meat that have been left in fresh water for six days, which thus have developed a strong odor of ammonia and are likely to contain harmful toxins.[1]

TASTING ABILITY IN HUMANS

In some human populations, we found a significant difference between the taste thresholds of men and women, especially in response to sodium chloride (Fig. 6, top) and oxalic acid (Fig. 7, bottom). Corresponding sex differences in taste ability among non-human primates have not yet been investigated. However, Galdikas and Teleki[107] suggested that differences in the feeding behavior of male and female pongids may have constituted the first evolutionary step toward a hominid division of labor. The different roles of men and women in subsistence activities is likely to result in distinct taste perceptions. For instance, the higher taste sensitivity for salt of Inuit women can be accounted for by a training effect: tasting and selecting ice for drinking water is traditionally a woman's task. A genetic basis for such differences cannot be excluded at present; however Hladik[108] has emphasized the very different time scales within which biological and cultural traits have evolved. Thus, the link between sexual differences in nonhuman primates and the cultural determinants of division of labor in present-day human societies is only tenuous.

In evolutionary terms, the retention of ancestral characteristics, together with recent adaptations, can be considered to constitute a common baseline in the feeding trends of various human populations. Fruits might have been the staple for hominids for a longer time than was previously suspected; an arboreal adaptation can be inferred from the foot bones of "Little Foot," a species of *Australopithecus* that lived in Africa three million years ago.[109] Jolly[110] presented a model of the transition, involving seed eating, from a frugivorous diet to a starchy diet of the incipient man. Feeding on grains, however, implies the seasonal storing of food, which requires a rather sophisticated technology. Alternatively, as has recently been demonstrated, the ability to feed on non-toxic tubers of yams, which are available in rain forests throughout the year, could have marked the beginning of starchy staple use.[111] The mild taste of starchy foods can explain the long-lasting practice of enhancing their palatability by adding other ingredients. Cooking, a further step in taste improvement, added substances like those created by the Maillard's reaction between amino acids and sugars on a roasting piece of meat.

A great number of taste carriers, including substances that normally are harmful in large amounts, can be simultaneously involved in any eating experience. Like bitter substances in beer, a bit of astringency, together with several aromatic volatiles, makes good wines. But, just with palm wine used throughout the tropical world,[112] symbolic values embedded in socioeconomic and cultural human environments shape food preferences beyond the convergence of taste, olfactory stimuli, and trigeminal information in the mammalian brainstem and beyond the psychosensory responses common to nonhuman primates.

ACKNOWLEDGMENTS

We thank R.A.A. Oldeman (Wageningen University), who read the first version of this paper and provided comments about the "beer-and-tobacco syndrome," John G. Fleagle and Kelly McNeese for their editorial contributions, and particularly Olga F. Linares (Smithsonian Tropical Research Institute), who clarified our text to make it palatable.

REFERENCES

1 Robbe P (1994) Les Inuit d'Ammassalik, Chasseurs de l'Arctique. Paris: Éditions du Muséum National d'Histoire Naturelle.

2 de Garine I (1993) Food resources and preferences in the Cameroonian forest. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 561–574. Paris: UNESCO-Parthenon Publishing Group.

3 Jolly A (1972) *The Evolution of Primate Behavior*. New York, Macmillan.

4 Hladik CM (1981) Diet and the evolution of feeding strategies among forest primates. In Harding RSO, Teleki G (eds), *Omnivorous Primates. Gathering and Hunting in Human Evolution*, pp 215–254. New York: Columbia University Press.

5 Whiten A, Widdowson E (eds) (1992) *Foraging Strategies and Natural Diets of Monkeys, Apes and Humans*. Oxford: Oxford University Press.

6 Van Buskirk RL, Erickson RP (1977) Odorant responses in taste neurons of the rat NTS. Brain Res *135*:287–303.

7 Stillman JA (1993) Color influences flavor identification in fruit-flavored beverages. J Food Sci *58*:810–812.

8 Rolls ET (1995) Central taste anatomy and neurophysiology. In Doty RL (ed), *Handbook of Olfaction and Gustation*, pp 549–573. New York: Marcel Dekker.

9 Schiffman SS, Erickson RP (1980) The issue of primary tastes versus a taste continuum. Neurosci Biobehav R *4*:109–117.

10 Faurion A (1987) Physiology of the sweet taste. In Otosson D (ed), *Progress in Sensory Physiology*, pp. 130–201. Heidelberg: Springer-Verlag.

11 Faurion A (1988) Naissance et obsolescence du concept de quatre qualités en gustation. J Agr Trad Bot Appl *35*:21–40.

12 Faurion A (1993) Why four semantic taste descriptors and why only four? 11th International Conference on the Physiology of Food and Fluid Intake, Oxford, July 1993:58.

13 Le Magnen J (1995) Gustation. In *Encyclopedia Universalis 11*, pp 83–87. Paris: Encyclopedia Universalis.

14 Nowlis GH, Frank ME (1977) Qualities in hamster taste:behavioral and neural evidence. In Le Magnen J, Mac Leod P (eds), *Olfaction and Taste VI*, pp 241–248. London: IRL.

15 Hofer OF, Meinel W, Sauer E (1990) Vergleichend-anatomische Untersuchungen an den Zungen von *Pan troglodytes* (Blumenbach, 1799) und weiteren Primates. Gegenbaurs Morphol Jahrb *136*:455–492.

16 Hellekant G, Ninomiya Y (1994) Bitter taste in single chorda tympani taste fibers from chimpanzee. Physiol Behav *56*:1185–1188.

17 Tonosaki K, Funakoshi M (1984) Intracellular taste cell responses of mouse. Comp Biochem Physiol *A 78*:651–656

18 Erickson RP, Covey E (1980) On the singularity of taste sensations. Physiol Behav *25*:527–533.

19 Steiner JE (1977) Facial expressions of the neonate infant indicating the hedonics of food-related chemical stimuli. In Weiffenbach JM (ed), *Taste and Development: The Genesis of Sweet Preference*, pp 173–189. Bethesda: U.S. Department of Health, Education and Welfare.

20 Steiner JE, Glaser D (1984) Differential behavioral responses to taste stimuli in nonhuman primates. J Hum Evol *13*:709–723.

21 Chiva M (1985) *Le Doux et l'Amer*. Paris, PUF.

22 Pfaffmann C (1960) The pleasures of sensation. Psychol Rev *67*:253–268.

23 Fantino M, Hosotte J, Apfelbaum M (1986) An opioid antagonist, naltrexone, reduces preference for sucrose in humans. Am J Physiol *251*:R91–R96.

24 Rolls BJ, Rolls ET, Rowe EA, Sweeney K (1981) Sensory specific satiety in man. Physiol Behav *27*:137–142.

25 Rolls ET, Sienkiewicz ZJ, Yaxley S (1989) Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. Eur J Neurosci *1*:53–60.

26 Cabanac M, Fantino M (1977) Origin of olfacto-gustatory alliesthesia: Intestinal sensitivity to carbohydrate concentration? Physiol Behav *18*:1039–1045.

27 Rabe E, Cabanac M (1974) Origine de l'alliesthésie olfacto-gustative: Effets comparés d'une huile végétale et du glucose intragastrique. CR Acad Sci Paris III *278*:765–768.

28 Louis-Sylvestre J, Le Magnen J (1980) A fall in blood glucose level precedes meal onset in free-feeding rats. Neurosci Biobehav R *4* (Suppl *1*):13–16.

29 Bellisle F, Lucas F, Amrani R, Le Magnen J (1984) Deprivation, palatability and the micro-structure of meals in human subjects. Appetite *5*:85–94.

30 Le Magnen J (1985) *Hunger*. Cambridge: Cambridge University Press.

31 Rolls BJ, Rolls ET (1982) *Thirst*. Cambridge: Cambridge University Press.

32 Garcia J, Koelling RA (1966) Relation of a cue to consequence in avoidance learning. Psychonom Sci *4*:123–124.

33 Brand JG, Kare MR, Naim M (1980) Restraints in accepting new foods: Relationships among taste, acceptability, and digestion. In Pearson PB, Greenwell JR (eds), *Nutrition, Food and Man. An Interdisciplinary Perspective*, pp 105–123. Tucson: The University of Arizona Press.

34 Rozin P (1990) Acquisition of stable food preferences. Nutr Rev *48*:106–113.

35 Simmen B, Hladik CM (1988) Seasonal variation of taste threshold for sucrose in a prosimian species, *Microcebus murinus*. Folia Primatol *51*:152–157.

36 Glaser D, Hellekant G (1977) Verhaltens und electrophysiologische Experimente über den Geschmackssinn bei *Saguinus midas tamarin* (Callitrichidae). Folia Primatol *28*:43–51.

37 Hladik CM, Robbe B, Pagezy H (1986) Sensibilité gustative différentielle des populations Pygmées et non Pygmées de forêt dense, de Soudaniens et d'Eskimos, en rapport avec l'environnement biochimique. CR Acad Sci Paris III *303*:453–458.

38 Hladik CM (1996) Perception des saveurs: Aspects méthodologiques de l'acquisition et de l'interprétation des données. In Froment A, de Garine I, Binam Bikoï C, Loung JF (eds), *Bien Manger et Bien Vivre. Anthropologie Alimentaire et Développement en Afrique Intertropicale:Du Biologique au Social*, pp 99–108. Paris: ORSTOM-L'Harmattan.

39 Hladik CM, Chivers DJ (1994) Foods and the digestive system. In Chivers DJ, Langer P (eds), *The Digestive System in Mammals: Food, Form and Function*, pp 65–73. Cambridge: Cambridge University Press.

40 Hladik CM (1977) Le régime alimentaire des primates et son adaptation aux ressources du milieu forestier. Thèse Doctorat d'Etat, Université Paris VI and Museum National d'Histoire Naturelle, Paris, France.

41 Simmen B, Sabatier D (n.d.) Diets of some French Guianan primates: Food composition and food choices. Int J Primatol, in press.

42 Simmen B, Hladik CM (n.d.) Sweet and bitter taste discrimination in primates: Scaling effects and phylogenetic relationships. Folia Primatol, in press.

43 Simmen B, Hladik CM (1993) Perception gustative et adaptation à l'environnement nutritionnel des primates non-humains et des populations humaines. Bull Mém Soc Anthropol Paris *5*:343–354.

44 Martin RD (1981) Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature *293*:57–60.

45 Martin RD, Chivers DJ, MacLarnon AM, Hladik CM (1985) Gastrointestinal allometry in primates and other mammals. In Jungers WL (ed), *Size and Scaling in Primate Biology*, pp 61–89. New York: Plenum.

46 Simmen B, Hladik CM, Martin RD (1995) Sweet and bitter taste discrimination and energy requirements in nonhuman primates. Chem Senses *20*:153.

47 Hladik CM (1979) Diet and ecology of Prosimians. In Doyle GA, Martin RD (eds), *The Study of Prosimian Behavior*, pp 307–357. New York: Academic Press.

48 Terborgh J (1983) Five New World Primates. A Study in Comparative Ecology. Princeton: Princeton University Press.

49 Simmen B (1992) Seuil de discrimination et réponses supraliminaires à des solutions de fructose en fonction du régime alimentaire des primates Callitrichidae. CR Acad Sci Paris III *315*:151–157.

50 Simmen B (1994) Taste discrimination and diet differentiation among New World primates. In Chivers DJ, Langer P (eds), *The Digestive System in Mammals: Food, Form and Function*, pp 150–165. Cambridge: Cambridge University Press.

51 Hladik CM (1993) Fruits of the rain forest and taste perception as a result of evolutionary interactions. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 73–82. Paris: UNESCO-Parthenon Publishing Group.

52 Hladik CM, Bahuchet S (1994) Perception and utilization of rain forest fruits and honey by the Aka Pygmies (Central African Republic). In Thierry B, Anderson JR, Roeder JJ, Herrenschmidt N (eds), *Current Primatology. Vol. I, Ecology and Evolution*. Selected Proceedings of the XIVth Congress of the International Primatological Society, pp 155–159. Strasbourg: Université Louis Pasteur.

53 Hladik CM (1988) Seasonal variations in food supply for wild primates. In Garine I de, Harrison GA (eds), *Coping with Uncertainty in Food Supply*, pp 1–25. Oxford: Clarendon Press.

54 Van der Wel H, van der Heijden A, Peer HG (1987) Sweeteners. Food Rev Int *3*:193–268.

55 Van der Wel H, Larson G, Hladik A, Hladik CM, Hellekant G, Glaser D (1989) Isolation and characterization of pentadin, the sweet principle of *Pentadiplandra brazzeana* Baillon. Chem Senses *14*:75–79.

56 Hladik CM, Hladik A (1988) Sucres et «faux sucres» de la forêt équatoriale : Évolution et perception des produits sucrés par les populations forestières d'Afrique. J Agr Trad Bot *35*:51–66.

57 Nash LT (1986) Dietary, behavioral, and morphological aspects of gummivory in primates. Yearb Phys Anthropol *29*:113–137.

58 Mela DJ, Langley KR, Martin A (1994) Sensory assessment of fat content: Effect of emulsion and subject characteristics.Appetite *22*:67–81.

59 Drewnowski A, Shrager EE, Lipsky C, Stellar E, Greenwood MRC (1989) Sugar and fat: Sensory and hedonic evaluation of liquid and solid foods. Physiol Behav *45*:177–183.

60 Perez C, Sclafani A (1990) Developmental changes in sugar and starch preferences in young rats. Physiol Behav *48*:7–12.

61 Sunderland G, Sclafani A (1988) Taste preferences of squirrel monkeys and bonnet macaques for polycose, maltose and sucrose. Physiol Behav *43*:685–690.

62 McKey D, Linares OF, Clement CR, Hladik CM (1993) Evolution and history of tropical forests in relation to food availability Background. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 17–24. Paris: UNESCO-Parthenon Publishing Group.

63 Glaser D (1986) Geschmacksforschung bei Primaten. Vjschr Naturf Ges Zürich *131/2*:92–110.

64 Haefeli RJ, Glaser D (1990) Taste responses and thresholds obtained with the primary amino acids in humans. Lebensm Wiss u Technol *23*:523–527.

65 Hladik CM (1977) A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In Clutton-Brock TH (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, pp 323–353. London: Academic Press.

66 Izawa K, Mizuno A (1977) Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates *18*:773–792.

67 Boesch C, Boesch H (1981) Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. J Hum Evol *10*:585–93.

68 Teleki G (1973) *The Predatory Behavior of Wild Chimpanzees*. Lewisburg: Bucknell University Press.

69 Kawamura Y, Kare MR (eds)(1987) *Umami: A Basic Taste*. New York: Marcel Dekker.

70 Hladik CM (1977) Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet. In Clutton-Brock TH (ed), *Primate Ecology:Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, pp 481–501. London: Academic Press.

71 Oates JF (1978) Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): A relationship with minerals and toxins in the diet ? Biotropica *10*:241–253.

72 Hladik CM, Gueguen L (1974) Géophagie et nutrition minérale chez les primates sauvages. CR Acad Sci Paris III *279*:1393–1396.

73 Johns T, Duquette M (1991) Detoxification and mineral supplementation as functions of geophagy. Am J Clin Nutr *53*:448–456.

74 Robbe B, Hladik CM (1994) Taste responses, food choices and salt perception among the Inuit of Greenland. In Thierry B, Anderson JR, Roeder JJ, Herrenschmidt N (eds), *Current Primatology. Vol. I, Ecology and Evolution*. Selected proceedings of the XIVth Congress of the International Primatological Society, pp 151–154. Strasbourg: Université Louis Pasteur.

75 Draper HH (1977) The aboriginal Eskimo diet in modern perspective. Am Anthropol *79*:309–316.

76 Speth JD (1987) Early hominid subsistence strategies in seasonal habitats. J Archaeol Sci *14*:13–29.

77 Pangborn RM, Chrisp RB, Bertolero LM (1970) Gustatory, salivary, and oral thermal responses to solution of sodium chloride at four temperatures. Percept Psychol *8*:69–75.

78 Whittaker RH, Feeny PP (1971) Allelochemics: Chemical interactions between species. Science *171*:757196770.

79 Rozin P (1976) The selection of food by rats, humans and other animals. In Rosenblatt J, Hinde RA, Beer C, Shaw E (eds), *Advances in the Study of Behavior, Vol. 6*, pp 21-76. New York: Academic Press.

80 Glander KE (1982) The impact of plant secondary compounds on primate feeding behavior. Yearbk Phys Anthropol *25*:1–18.

81 Huffman MA, Seifu M (1989) Observations on the illness and consumption of a possibly medicinal plant, *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania. Primates *30*:51–63.

82 Harris H, Kalmus H (1949) The measurement of taste sensitivity to phenylthiourea (PTC). Ann Eugenics *15*:24–31.

83 Reddy BM, Rao DC (1989) Phenylthiocarbamide taste sensitivity revisited: Complete sorting test supports residual family resemblance.Genet Epidemiol *6*:413–421.

84 Jackson FLC (1993) The influence of dietary cyanogenic glycosides from cassava on human metabolic biology and microevolution. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 321–338. Paris: UNESCO-Parthenon Publishing Group.

85 Boyce AJ, Harrison GA, Platt CM, Hornabrook RW (1976) Association between PTC taster status and goitre in a Papua New Guinea population. Hum Biol *48*:769–773.

86 Koshimizu K, Ohigashi H, Huffman MA, Nishida T, Takasaki H (1993) Physiological activities and the active constituents of potentially medicinal plants used by wild chimpanzees of the Mahale Mountains, Tanzania.Int J Primatol *14*:345–356.

87 Dufour DL (1993) The bitter is sweet: A case study of bitter cassava (*Manihot esculenta*) used in Amazonia. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 575–588. Paris: UNESCO-Parthenon Publishing Group.

88 Swain T (1979) Tannins and lignins. In Rosenthal GA, Janzen DH (eds), *Herbivores, Their Interaction with Secondary Plant Metabolites*, pp 657–682. New York: Academic Press.

89 Hellekant G, Hladik CM, Dennys V, Simmen B, Roberts TW, Glaser D, DuBois G, Walters DE (1993) On the sense of taste in two Malagasy primates (*Microcebus murinus* and *Eulemur mongoz*). Chem Senses *18*:307–320.

90 Ganzhorn JU (1989) Primate species separation in relation to secondary plant chemicals. Hum Evol *4*:125–132.

91 Bryant BP, Moore PA, O'Bannon Y (1994) Oral trigeminal chemoreception of acidic irritants: Role of the epithelium, neural coding and behavioral correlates. Proceedings of the 11th ECRO Congress, Blois, France:225.

92 Glaser D, Hobi G (1985) Taste responses in primates to citric and acetic acid. Int J Primatol *6*:395–398.

93 Ungar PS (1995) Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. Int J Primatol *16*:221–245.

94 Schifferstein HNJ, Frijters JER (1990) Sensory integration in citric/acid sucrose mixtures. Chem Senses *15*:87–109.

95 Milton K, Jenness R (1987) Ascorbic acid content of neotropical plant parts available to wild monkeys and bats. Experientia *43*:339–342.

96 Waterman PG (1984) Food acquisition and processing as a function of plant chemistry. In Chivers DJ, Wood BA, Bilsborough A (eds), *Food Acquisition and Processing by Primates*, pp 177–211. New York: Plenum Press.

97 de Garine I, Harrison GA (eds.) (1988). *Coping with Uncertainty in Food Supply*. Oxford: Clarendon Press.

98 de Garine I (1980) Approaches to the study of food and prestige in savanna tribes, Massa and Mussey of Northern Cameroon and Chad. Soc Sci Info *19*:39–78.

99 Pasquet P, Brigant L, Froment A, Koppert G, Bard D, Garine I de, Apfelbaum M (1992) Massive overfeeding and energy balance in men: The Guru Walla model. Am J Clin Nutr *56*:483–490.

100 Koshimizu K, Ohigashi H, Huffman MA (1994) Use of *Vernonia amygdalina* by wild chimpanzee: Possible roles of its bitter and related constituents. Physiol Behav *56*:1209–1216.

101 Mahaney WC, Aufreiter S, Hancock RGV (1995) Mountain gorilla geophagy: A possible seasonal behavior for dealing with the effects of dietary changes. Int J Primatol *16*:475–488.

102 Rozin P, Kalat JW (1971) Specific hungers and poison avoidance as adaptive specializations of learning. Psychol Rev *70*:459–485.

103 Hugh-Jones S (1993) «Food» and «drugs» in Northwest Amazonia. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 533–548. Paris: UNESCO-Parthenon Publishing Group.

104 Johns T (1990) *With Bitter Herbs They Shall Eat It. Chemical Ecology and the Origins of Human Diet and Medicine*. Tucson: The University of Arizona Press.

105 Delluc G, Delluc B, Roques M (1995) *La Nutrition Préhistorique*. Périgueux: Pilote 24.

106 Goodall J (1986) *The Chimpanzees of Gombe. Patterns of Behavior*. Cambridge, The Belknap Press of Harvard University Press.

107 Galdikas BMF, Teleki G (1981) Variations in subsistence activities of female and male pongids: New perspectives on the origins of hominid labor division. Curr Anthropol *22*:241–256.

108 Hladik CM (1995) Différenciation sexuelle du comportement alimentaire chez les Primates non humains et chez l'Homme. In Ducros A, Panoff M (eds), *La Frontière des Sexes*, pp 73–103. Paris: PUF.

109 Clarke RJ, Tobias PV (1995) Sterkfontein Member 2 foot bones of the oldest South African hominid. Science *269*:521–524.

110 Jolly CJ (1970) The seed-eaters: A new model of hominid differentiation based on a baboon analogy. Man *5*:5–26.

111 Hladik A, Dounias E (1993) Wild yams of the African forest as potential food resources. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 163–176. Paris: UNESCO-Parthenon Publishing Group.

112 Linares OF (1993) Palm oil versus palm wine:symbolic and economic dimensions. In Hladik CM, Hladik A, Linares OF, Pagezy H, Semple A, Hadley M (eds), *Tropical Forests, People and Food: Biocultural Interactions and Applications to Development*, pp 595–606. Paris: UNESCO-Parthenon Publishing Group.